

PHENOTYPIC PLASTICITY IN *SCENEDESMUS*: IMPLICATIONS FOR ALGAL TAXONOMY AND ECOLOGY

PLASTICIDAD FENOTIPICA EN SCENEDESMUS: SUS IMPLICACIONES EN LA TAXONOMIA Y ECOLOGIA DE LAS ALGAS

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ABSTRACT

Phenotypic plasticity, the ability of a genotype to produce morphological alternatives under differing environmental situations, has been repeatedly reported in the biological literature. However, the taxonomical, ecological, and evolutionary implications of plasticity have not been adequately recognized. Traditional classification schemes based almost entirely on morphological characters do not reflect natural relationships among organisms due to lack of considerations on plasticity, one of the most important qualities of life. Substantial data on the green algal genus *Scenedesmus* put in evidence the impact of plasticity on taxonomy at the varietal, specific, and generic levels, suggesting possible multidisciplinary alternatives for the construction of more natural classification schemes.

KEYWORDS: Plasticity, *Scenedesmus*, ecology.

RESUMEN

La plasticidad fenotípica, definida como la capacidad de un genotipo para la producción de alternativas morfológicas en respuesta a variaciones medioambientales, ha sido reportada en varias ocasiones en la literatura biológica. A pesar de ello, sus implicaciones taxonómicas, ecológicas y evolucionarias no han sido reconocidas apropiadamente. Sistemas de clasificación basados principalmente en aspectos morfológicos no reflejan afinidades naturales entre los organismos al carecer de consideraciones sobre la plasticidad fenotípica, una de las cualidades más importantes de la vida. Datos substanciales colectados en el género de algas verdes *Scenedesmus* ponen en evidencia el impacto que la plasticidad fenotípica tiene sobre la taxonomía a nivel de variedades, especies y géneros, sugiriendo al mismo tiempo posibles alternativas multidisciplinarias para la construcción de esquemas clasificatorios más naturales.

PALABRAS CLAVES: Plasticidad, *Scenedesmus*, ecología.

INTRODUCTION

Due to their polyphyletic origin, the algae are composed of a widely diverse array of organisms that differ extensively at both morphological and physiological levels. Such diversity led early phycologists to resolve organismal affinities based on practical techniques that allowed for the analysis of large numbers of specimens in short periods of time. With little recognition of improvements in either ecological approaches or in culture of

organisms in the laboratory, algal taxonomy and systematics grew within an inflexible framework focused on "appearance", but lacking concepts of "function". The use of cultures allowed for detailed studies of life histories and the discovery of phenotypic plasticity, a rather frequent process that traditional field techniques had not been able to recognize. Yet, there appears to be a reluctance to expand species protologies and many new taxa are still being erected based on preserved (inert) material.

PHENOTYPIC PLASTICITY: CONCEPT AND MECHANISM

Phenotypic plasticity refers to the ability of a single genotype to produce several phenotypes under

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fluctuating environmental conditions. This change in phenotype occurs on the same individual in organisms having indeterminate growth (the majority of plants), or in subsequent generations in organisms having determinate growth (the majority of animals and protists). The plasticity would include not only the characters we presently take for granted, e.g., a size range for a taxon, or more than one mechanism for reproducing, but also remarkable alterations in either size or the ability to turn certain cytological features on or off (Schlichting & Pigliucci, 1998; Trainor, 1998).

Although asexually reproducing organisms provide a better understanding of plasticity due to the genetically homogeneous background, sexually reproducing entities also exhibit plasticity. In fact, sexually reproducing populations tend to have a high degree of polymorphism (genetic diversity) due to recombination, providing genetic variability for plastic responses. The consideration of plasticity as a trait is not new to science (Schlichting, 1986; Via & Lande, 1985) and some recent research has focused on the study of "plasticity genes" (e.g., Ballarè *et al.*, 1990; Hubel & Schoffl, 1994) and patterns in their operation.

Recent genetic and molecular studies have yielded crucial information about the mechanism of plasticity at the gene level (e.g., Guttenbrunner *et al.*, 1994; Mazel & Marliere, 1989; Santoni *et al.*, 1994). These studies put forward the idea that genes can no longer be considered as "blueprints" of organisms, for there are multiple processes that may remodel characters before, during, and after transcription (Pigliucci, 1996). The discovery of homeobox genes, and the development of the concept of epigenesis, the molding of characters through gene interaction or non-genetic events such as hormone action and cell to cell communication (Waddington, 1975; Schlichting & Pigliucci, 1998), suggests that the rise of phenotypes is far more complicated than previously thought (Fig. 1). The origin of emergent properties as a result of gene interaction and the dependence of these properties on internal (within the cell) and external environments, enable organisms to respond with different phenotypic options to fluctuations in the environment. In the light of this evidence, the belief that species exhibit only limited variation around a typical morphology lacks support. Thus, the dogma "one morph, one taxon" ought not to continue to be used as the foundation of algal classification systems. Evidence shows that

plasticity is not a feature of merely a few genotypes, a "peculiarity" of *Scenedesmus*, or an outcome of experimental error, but rather a widespread phenomenon. Plasticity is a universal quality of life (West-Eberhard, 1989) that should be incorporated into taxonomic considerations of living organisms.

In order to realize how a variant phenotype is produced we must first understand that not all the genetic information contained in an individual is used at one time (Oliver, 1996; Ridley, 1996; Smith *et al.*, 1996). This is, genes are turned on and off by the action of master switches (homeobox genes) following environmental shifts. Thus, the organism "uses" those regions in the DNA that provide the most appropriate characters under prevailing habitat conditions. If conditions change, some other regions are turned on producing a new physiological state frequently associated with a morphological change (Jacob & Monod, 1961; Meins & Binns, 1979; Santoni *et al.*, 1994).

Two types of genetic control of plasticity have been recognized (Schlichting & Pigliucci, 1993, 1995). First, allelic sensitivity is characterized by a gradual modification of gene action unchaining a progressive change in the phenotype of the individual. This kind of genetic response to environmental change is derived from the effect of factors such as temperature, pH, and alcohol concentration on the chemical activity of enzymes (see Schlichting & Pigliucci, 1998 for a review on the subject). Although this mechanism may not be readily distinguished from acclimation, we propose that during the latter there is a phenotypic change within the range of tolerance of the organisms to particular environmental conditions. When physiological limits imparted by operating genes are disrupted, the organism produces a new phenotype implemented with a novel range of tolerance.

The second form of genetic control of plastic responses is called gene regulation. During this process, there is a drastic change in the phenotype of the individual (polyphenism) produced by expression of environment-specific genes (Smith, 1990; Schlichting & Pigliucci, 1998). Although experimental evidence at the genetic level is not yet available, gene regulation might be the mechanism triggering the production of ecomorphs (environmentally induced phenotypes) in *Scenedesmus*, where each ecomorph is expressed under specific physical, chemical, and biological (presence of predators) conditions in the extracellular environment.

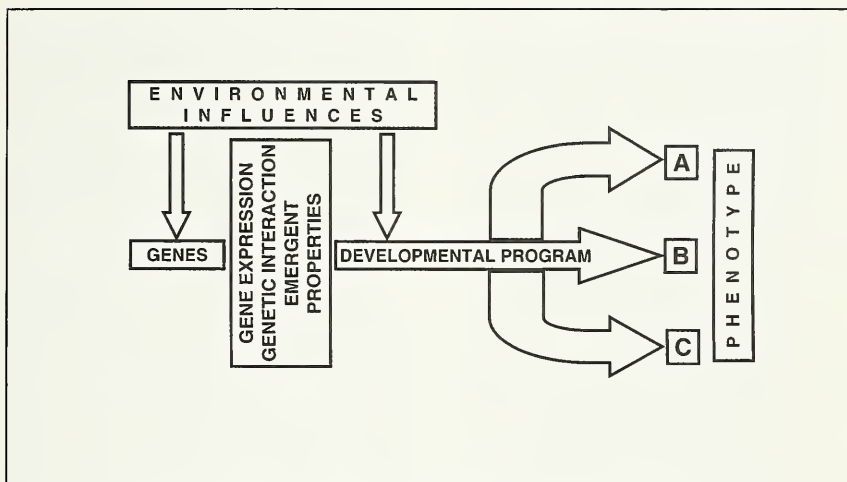


FIGURE 1. The complex mechanism by which a genotype produces a phenotype. Environmental influences at the genetic level change "normal" patterns of gene expression, the way genes interact, and the emergent properties that originate from such interactions. Changes in external and internal conditions at the time of development, are also likely to produce alterations in the final phenotypic outcome.

FIGURA 1. El complejo mecanismo mediante el cual un genotipo produce un fenotipo. Influencias ambientales en los cambios a nivel genético en los patrones "normales" de expresión genética, la forma en que los genes interactúan y las propiedades emergentes que originan tales interacciones. Los cambios en las condiciones externas e internas durante el período de desarrollo también podrían producir alteraciones en el fenotipo final.

ECOLOGICAL IMPLICATIONS OF PHENOTYPIC PLASTICITY

Organisms must be able to deal with spatial and temporal heterogeneity in their habitats. Such heterogeneity will determine the patterns of distribution of organisms and the type of strategy needed for survival. The spatial heterogeneity problem may bring about two different solutions. First, if a population is genetically variable (polymorphic), and if genotypes have a low degree of phenotypic plasticity, then ecotypes will arise by natural selection. These ecotypes are genetically distinct and locally adapted sectors of the population that grow better under a particular set of environmental parameters. Outside these local conditions, fitness of these ecotypes will be severely affected resulting in poor growth or increased mortality (Clausen *et al.*, 1947, 1948). Second, if

the population is plastic, and whether or not this plasticity is enhanced by polymorphism (asexual vs. sexual populations), a generalist strategy will be adopted. Generalists will be able to colonize a wide range of habitats, responding to environmental changes by production of an adaptive ecomorph. This ecomorph is a phenotypically (not genetically) distinct individual, and once prevailing conditions are changed it will be able to produce a new ecomorph (Egan & Trainor, 1989).

To understand the process of adaptation to temporal variation, two aspects must be considered. First, single individuals may be exposed to environmental change at some point(s) in their lifetime (fine-grained variation). And second, environmental change may be produced at intervals greater than the life span of individuals (coarse-grained variation) (Levins, 1968; MacArthur & Levins, 1967). Adaptation to fine-grained variation may occur by acclimation or

plasticity controlled by either allelic sensitivity or gene regulation. Acclimation is defined here as a small adjustment in the phenotype triggered by environmental changes that do not transgress the range of tolerance to a particular condition. Since the phenotypic response is a result of a gene-environment interaction, acclimation may be considered as a type of plasticity. As stated previously during allelic sensitivity or gene regulatory processes, a phenotypic variant will be produced as soon as the range of tolerance is disrupted by the environmental change.

Coarse-grained variation in habitat conditions will trigger plastic responses from populations, where the phenotypic change will be evident in the following generation. Polymorphism may also be maintained in cases in which environmental change is produced in a cyclic fashion (Karlin & Levikson, 1974), producing a "succession" of genotypes over the period of ecological change. In summary, we can state that the interplay between polymorphism and plasticity adds to the capability that populations have to deal with environmental impositions.

PHENOTYPIC PLASTICITY IN *SCENEDESMUS*

When organisms within the green algal genus *Scenedesmus* are exposed to changes in culture conditions either in the laboratory or in the field, an ordered sequence of ecomorph production is manifested (Egan & Trainor, 1989; Trainor, 1965, 1976, 1979, 1995). It has been suggested recently that this sequence could have an adaptive advantage under grazing pressures (Lürling, 1999). Additionally, the adaptiveness of each of the ecomorphs becomes clear when situations of nutrient distribution, seasonality, and density-dependent phenomena are taken into consideration. We present a summary and implications of many years of research in the following pages.

In temperate freshwater ecosystems, the production of unicellular morphs coincides with the beginning of the growing season (spring). At this time of the year, the water column contains high concentrations of nutrients and population density is small. Unicells allow the population to cover a wider area in the habitat,

maximizing interspecific competition and reducing intraspecific competition considerably. Allometric relationships between surface area and volume of the cell allow unicellular morphs to capture more nutrients per unit time, maintaining individuals in the photic zone (Lürling, 1998). Grazing is not an important force acting on the algal population at this time of the year since zooplankton densities are low (Steinberg & Geller, 1994; Trainor & Egan, 1990).

By the time the population approaches its carrying capacity, concentrations of nutrients, and temperatures in the water column have decreased considerably, and shorter days are characteristic (late summer or early fall). Densities of predator populations also increase, having a significant grazing impact on algal populations. In the absence of effective movement in *Scenedesmus* with respect to predators, natural selection has favored the development of a predator-avoidance mechanism that involves an augmentation of size through formation of four-celled or eight-celled colonies. These morphs often exceed the food size range required by predators (Hessen & Van Donk, 1993; Lürling & Van Donk, 1996).

There is recent evidence suggesting that colony formation is triggered by compounds released by the predators to the aquatic medium (Lürling, 1998, 1999). However, the possibility that such compounds might have their origin in other members of a population responding to predation is still open (Lürling, 1998; Lürling & Van Donk, 1997). Colonies formed under these circumstances are equipped with long spines and multiple bristles that also act as antipredator devices by increasing the surface area of individual colonies. Other less studied mechanisms of predator-avoidance are the aggregation of cells around mucous exudates and fecal pellets from the predator (Lürling & Van Donk, 1997).

Spines and bristles are also aids in flotation, increasing friction with water molecules. Additionally, it has been demonstrated that bristles confer on colonies a positive phototactic movement maintaining populations in the photic zone (Burg & Trainor,

1967; Conway & Trainor, 1972; Trainor, 1966; Trainor & Massalski, 1971). Buoyancy of colonies is also increased by a production of fatty acids within cells (Lüring *et al.*, 1997). Since population densities are high at this stage of development, intraspecific and interspecific competition are also very high. Under these conditions, spines and bristles could provide a means for increased nutrient absorption (Conway & Trainor, 1972); and at the same time, could act as "spacers" between adjacent colonies.

By the end of fall, temperatures in the water have decreased even further, nutrients have been almost depleted, and photoperiod has changed considerably. Under these conditions, spineless (or short-spined) colonies heavily ornamented with ridges are produced. These colonies have a much higher tendency to sink, and thus constitute dormant stages that are stored at the bottom of lakes until better habitat conditions develop (Conway & Trainor, 1972; Egan & Trainor, 1989). Besides contributing to an increase in weight of the colony, ridges may serve in the aggregation of several colonies accelerating sinking rates (Massalski & Trainor, 1971).

At the beginning of the next growing season, once nutrients are replenished and photoperiod and water temperatures are optimal for growth, bicellular and tetracellular coenobia are produced. Both of these morphs possess spines that are longer than the length of the cell. Tetracellular coenobia produced at this point (type I colonies) are different from tetracellular coenobia arising from unicells (type II colonies) (Egan & Trainor, 1989). The role of these two-celled and four-celled colonies is to migrate to the photic zone and produce unicells beginning the cycle once more (Egan & Trainor, 1989).

These succession of phenotypes is ordered in the sense that only type I colonies are able to produce unicells, only unicells are capable of producing type II colonies, and so on (Fig. 2). However, erratic environmental changes and microhabitat formation in ecosystems truncate the sequence at different points. Thus, while a portion of the population is in the unicellular stage, another portion could be in the form of spineless coenobia.

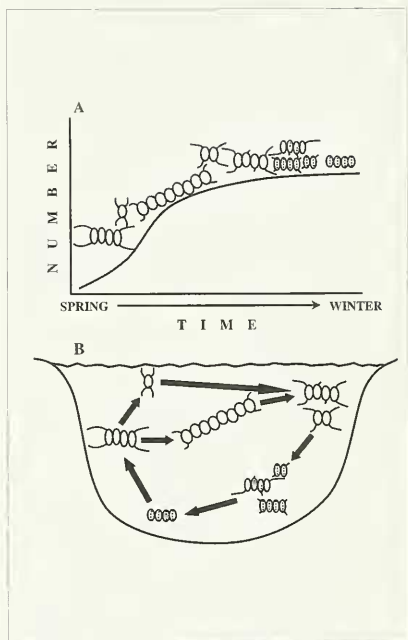


FIGURE 2. The ordered sequence of ecomorphs formation in a spiny *Scenedesmus* species. A. The production of the different ecomorphs is dependent on cell densities and habitat conditions during the year. B. Such morphs occupy specific sites in the aquatic ecosystem.

FIGURA 2. La secuencia ordenada de formación de ecomorfos en una especie espinosa de *Scenedesmus*. A. La producción de los distintos ecomorfos depende de las densidades de células y las condiciones ambientales durante el año. B. Dichos morfos ocupan hábitats específicos en el ecosistema acuático.

TO BE OR NOT TO BE...

Although there still is some resistance among researchers to incorporate the concept in current research, plasticity has been an implicit aspect of biological research for many years. Processes of alternation of generations, leaf dimorphism, cell differentiation, etc., imply changes in form in one way or another. Despite ploidy arguments against the

recognition of alternation of heteromorphic generations as an example of plasticity, there is no evidence showing that a mere change in the amount of genetic material would turn a gametophyte into a sporophyte (or vice versa). Rather, specific cDNAs (derived from mRNA) might be controlling changes in morphology in both stages (Liu *et al.*, 1994). This explanation fits into our previous explanation of the role of epigenetics in the formation of new phenotypes. As the number of genes available is either increased or decreased, substantial modifications in emergent properties will unchain equally profound phenotypic modifications. In fact, recent studies have shown the extreme importance of gene and chromosome duplication in evolutionary processes (see Schlichting & Pigliucci, 1998 for further discussion).

History has taught us the taxonomical implications of life histories involving alternation of heteromorphic generations. We now know for example, that the genera *Bangia* and *Conchocelis* are but different generations of the same species, and that the change from one to another is triggered by photoperiod (Conway & Cole, 1977; Dixon & Richardson, 1969; Drew, 1949). What is more, several other species within *Bangia*, and even within other genera such as *Porphyra*, include a *Conchocelis*-like phase as part of their life history (Fukuhara, 1968). This is reminiscent of the fact that several species of *Scenedesmus* also share the quadricaudate stage (type II colonies) of the ordered sequence of ecomorph expression (see later) (Trainor, 1991, 1996).

Leaf dimorphism or heterophylly is also an example of phenotypic plasticity that has been immersed in biological literature for a long time (Arber, 1919). Aquatic plants such as *Ranunculus* spp. are able to produce significantly different submerged and aerial leaves, each one having anatomical adaptations to suit prevalent environmental conditions (Cook, 1968).

One of the most remarkable examples of plasticity is cell differentiation in eumetazoans and plant cells. The high degree of plasticity characterizing embryonic cells determines the formation of the multiple cell types present in tissues of adult organisms. Recent developments

in biotechnology have demonstrated that a single meristematic cell is capable of producing a complete individual. Cases of animal phenotypic plasticity have been documented for gastropods (Bailey & Moore, 1986; Bosman & Hockey, 1988), insects (Baldwin & Dingle, 1986), fish (Stearns & Crandall, 1984), amphibians (Kaplan, 1987), reptiles (Ford & Seigel, 1989), etc., giving further evidence on the universality of plastic processes. On the other hand, studies on species in the genera *Phlox* and *Arabidopsis* are among the most prominent investigations of phenotypic plasticity in higher plants (Pigliucci *et al.*, 1995; Schlichting & Levin, 1984).

IMPROVING EXISTING CLASSIFICATION SYSTEMS

Taxonomical implications of plasticity are obvious. In the case of *Scenedesmus*, ecomorphs have received different varietal, specific, and even generic names. The term variety has been highly misused in scenedesmolology and evidence concerning the genetic nature of such "varieties" has not been provided at the time of description. There has also been a tendency to assign varietal ranks to single strains assuming genetic variation, but supporting data based on careful experimentation in the laboratory is usually lacking. At the species level, different epithets have been assigned to ecomorphs that seem to be a common stage in the life history of several *Scenedesmus* species. In the concrete case of type II colonies (tetracellular coenobia with long spines), the name *S. quadricauda* has been indiscriminately applied (Fig. 3) (Trainor, 1991).

At the genus level the problem seems most acute. Unicellular ecomorphs have been placed in *Chodatella* or *Franceia*, and systems based on these erroneous taxonomic decisions are still being used to this date (see discussion in Trainor, 1998). Colonial morphs in which cells form chains by joining their apical ends have been ascribed to *Dactylococcus*, a genus that now needs major revisions in the light of *Scenedesmus* research (Chodat, 1926; Grunow, 1858; Trainor 1963).

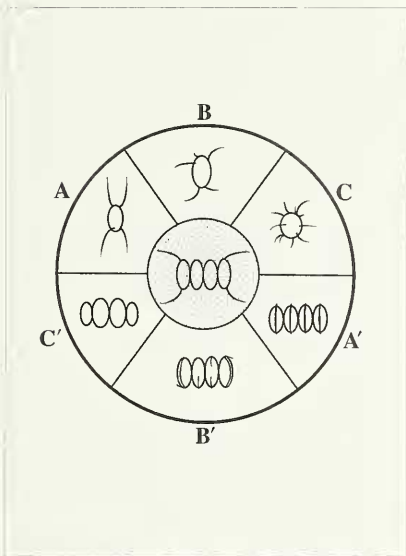


FIGURE 3. Diagrammatic representation of the beginning, middle, and end points in the ordered sequence of ecomorph production for three species of *Scenedesmus*. The sequence A-A' represents *S. armatus* (strain 2193) (Egan & Trainor, 1989); B-B' represents strain N 56 (Trainor & Roskosky, 1967); and C-C' represents *S. kissii* (UTEX 831) (Trainor, 1995). The central circle indicates that there is a production of a quadricaudate morph that can not be assigned with certainty to any of the three species if found in isolation.

FIGURA 3. Representación diagramática de las etapas iniciales, intermedias y finales en la secuencia ordenada de ecomorfos para tres especies de *Scenedesmus*. La secuencia A-A' representa *S. armatus* (cepa 2193) (Egan & Trainor, 1989), B-B' representa la cepa N 56 (Trainor & Roskosky, 1967) y C-C' corresponde a *S. kissii* (UTEX 831) (Trainor, 1995). El círculo central indica la producción de un morfo cuadricaudato que no puede asignarse con certeza a cualquiera de las tres especies si se encuentra de forma aislada.

The most recent catalogue on the genus *Scenedesmus* (Hegewald & Silva, 1988) includes around 1300 taxa, but conservative estimations based on plasticity research point to the synonymy of at least 60% of these taxa (Trainor, 1998). Similar measures have already been taken in the case of cyanobacteria. Of the 2800 species of coccoid blue

greens, Drouet & Daily (1956) only recognized 32 as true species. Although there is concern about the methodology utilized by these authors, subsequent research has demonstrated that cyanobacteria is indeed a very plastic group (Jeeji-Bai, 1977; Lazaroff & Vishniac, 1961; Robinson & Miller, 1970; Stein, 1963; etc.).

Plasticity has also been reported for diatoms (Lewin *et al.*, 1958; Schmid, 1979; Schultz, 1971; Stoermer, 1967; etc.), but the appreciation of implications at the taxonomical level is hindered by widespread use of acid-clean material in the description of taxa. The strong advocacy for the use of morphological features among diatomists has been strengthened by development of the scanning electron microscope (Round, 1996) and ecological methodologies making use of inert material (Battarbee, 1986). Taxonomical considerations in this group are presumably further complicated by morphological variations due to frustule size reduction and polymorphism (Cox, 1993). Varietal names have also been used extensively without fair assessment of the genetic nature of the morphological variability. Evidence is provided, for example, by the frequent finding of several varieties of fragilarioid or eunotioid taxa in single samples. At the species level, the work of Stoermer (1967) in *Mastogloia* has demonstrated that what had been considered distinct populations, were in fact morphological expressions of single genotypes.

It is evident that much more research focused on the biology of species will provide better grounds for classification systems. This type of approach has been successfully applied in the case of bacteria, in which biochemical and physiological characters became crucial in classification and identification procedures. The use of the electron microscope may also lead to characterization of more reliable features for species delimitation (Bisalputra & Weier, 1963; Komárek & Ludvik, 1971; Pickett-Heaps, 1975). However, the use of this kind of information in scenedesmology -and in other algal groups- is only beginning to be understood (Trainor, 1996). Additionally, although the value of molecular studies has been recognized (Kessler *et al.*, 1997), these data are still quite limited, as attention has been diverted elsewhere.

Traditional morphologically based classification systems have demonstrated to be very useful and practical. However, they include a strong anthropomorphic bias and do not reflect real biological, ecological, and evolutionary aspects of organisms. Morphology is simply an outcome of gene expression; thus, attention should concentrate on

the mechanisms of such gene expression and how individual genes are affected by internal and external environmental influences. More natural and reliable classification systems can be constructed only by the integration of multidisciplinary research.

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